Intake, selection, digesta retention, digestion and gut fill of two coprophageous species, rabbits (Oryctolagus cuniculus) and guinea pigs (Cavia porcellus), on a hay-only diet

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Abstract: A colonic separation mechanism (CSM) is the prerequisite for the digestive strategy of coprophagy. Two different CSM are known in small herbivores, the 'wash-back' CSM of lagomorphs and the 'mucous-trap' CSM of rodents. Differences between these groups in their digestive pattern when fed exclusively hay were investigated in six rabbits (Oryctolagus cuniculus) and six guinea pigs (Cavia porcellus). Intake, digestibility (by total faecal collection), solute and particle mean retention times (MRT, using Co-EDTA and Cr-mordanted fibres) were measured. Rabbits selected less fibrous parts of the hay than guinea pigs, leaving orts with higher content of neutral detergent fibre [NDF; 721 ± 21 vs. 642 ± 31 g/kg dry matter (DM) in guinea pigs]. They also expressed a lower NDF digestibility (0.44 ± 0.10 vs. 0.55 ± 0.05 of total), a similar particle MRT (15 ± 3 vs. 18 ± 6 h), a longer solute MRT (51 ± 9 vs. 16 ± 4 h), and a lower calculated dry matter gut fill (19.6 ± 4.7 vs. 29.7 ± 4.1 g DM/kg body mass) than guinea pigs ($p < 0.05$ for each variable). These results support the assumption that the 'wash-back' CSM, exhibited in the rabbits, is more efficient in extracting bacterial matter from the colonic digesta plug than the 'mucous-trap' CSM found in the guinea pigs. Related to metabolic body mass, rabbits therefore need a less capacious colon for their CSM where a more efficient bacteria wash-out is reflected in the lower fibre digestibility. A lighter digestive tract could contribute to a peculiarity of lagomorphs: their ability to run faster than other similar-sized mammals.

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Summary

A colonic separation mechanism (CSM) is the prerequisite for the digestive strategy of coprophagy. Two different CSM are known in small herbivores, the 'wash-back' CSM of lagomorphs and the 'mucous-trap' CSM of rodents. Differences between these groups in their digestive pattern when fed exclusively hay were investigated in six rabbits (*Oryctolagus cuniculus*) and six guinea pigs (*Cavia porcellus*). Intake, digestibility (by total faecal collection), solute and particle mean retention times (MRT, using Co-EDTA and Cr-mordanted fibres) were measured. Rabbits selected less fibrous parts of the hay than guinea pigs, leaving orts with higher content of neutral detergent fibre (NDF; 721 ± 21 vs. 642 ± 31 g/kg dry matter (DM) in guinea pigs). They also expressed a lower NDF digestibility (0.44 ± 0.10 vs. 0.55 ± 0.05 of total), a similar particle MRT (15 ± 3 vs. 18 ± 6 h), a longer solute MRT (51 ± 9 vs. 16 ± 4 h), and a lower calculated dry matter gut fill (19.6 ± 4.7 vs. 29.7 ± 4.1 g DM/kg body mass) than guinea pigs ($p < 0.05$ for each variable). These results support the assumption that the 'wash-back' CSM, exhibited in the rabbits, is more efficient in extracting bacterial matter from the colonic digesta plug than the 'mucous-trap' CSM found in the guinea pigs. Related to metabolic body mass, rabbits therefore need a less capacious colon for their CSM where a more efficient bacteria wash-out is reflected in the lower fibre digestibility. A lighter digestive tract could contribute to a peculiarity of lagomorphs: their ability to run faster than other similar-sized mammals.

Introduction

In many small mammalian herbivores – mainly represented by lagomorphs (rabbits, hares and pikas) and rodents – the practice of coprophagy has been documented (Kenagy and Hoyt, 1980; Hirakawa, 2001, 2002). Actually, it was suggested that this digestive strategy should be assumed to occur in any lagomorph or herbivorous rodent until the opposite is proven (Clauss et al., 2007a). Coprophagy ensures that protein synthesised by bacteria growing in the distal fermentation chambers, the caecum and the colon, is not lost via defaecation but reingested. Additionally, other bacterial products like vitamins or undigested remains of essential nutrients like fatty acids are used by the herbivore in this way (Karasov and Martínez del Rio, 2007; Leiber et al., 2008). Coprophagy appears to occur only in small herbivores, with the largest known coprophageous animal being the largest rodent, the capybara (*Hydrochaeris hydrochaeris*) (Hirakawa, 2002). One reason for this association with size may be that small herbivores cannot compensate for metabolic losses on low-quality forage by using body reserves, and thus have to maintain high food intakes on low-quality forages and minimize metabolic losses via coprophagy (Meyer et al., 2010).

A prerequisite for the practice of coprophagy is a mechanism in the digestive tract that separates the valuable material (mainly bacteria and small particles) from indigestible or hardly digestible residues, i.e. a 'colonic separation mechanism' (CSM) (Björnhag, 1987). Basically, two types of CSM exist (Cork et al., 1999): a 'wash-back' CSM as found in lagomorphs, and a 'mucus-trap' CSM as found in rodents. The colon of lagomorphs is characterised by three taenia and haustrae in the first, and one taenia with haustrae in the second part of the proximal colon; fluid secretion and retrograde peristalsis occurs during the phase when hard faeces are formed (Clauss, 1978; Snipes et al., 1982; Ehrlein et al., 1983). Thus, fluids, bacteria and small particles are washed back into the caecum. Different from that, the colon of caviomorph and hystricomorph rodents is equipped with a peculiar anatomical structure, the 'colonic groove' or 'furrow' (Gorgas, 1966; Snipes et al., 1988). In

73 this groove, mucous and bacteria are trapped and transported back to the caecum (Holtenius
74 and Björnhag, 1985; Takahashi and Sakaguchi, 2000, 2006). The colon of some myomorph
75 rodents is characterised by anatomical structures like longitudinal folds and oblique furrows
76 (*Plicae circulares*) that may serve a similar purpose as the colonic groove in caviomorph
77 rodents (Behmann, 1973; Sperber et al., 1983). The CSM type can be differentiated by the use
78 of passage markers (Cork et al., 1999; Pei et al., 2001): The 'wash-back' CSM is
79 characterised by short particle but long fluid retention times, whereas the 'mucus trap' CSM
80 results in a more or less simultaneous excretion of fluid and particle passage markers.
81 The question whether the two CSMs differ in more than the fluid retention pattern has been
82 hardly addressed (Björnhag and Snipes, 1999). Discussions of this topic focus mainly on the
83 appearance of the faeces. In lagomorphs, two different types of faeces are formed: the so-
84 called 'hard' faeces, which are mostly not re-ingested and which consist of larger particles,
85 and the so-called 'soft' faeces or 'caecotrophs' that are re-ingested (Hirakawa, 2001). In
86 contrast, such a separation of faeces types is considered less evident in rodents (Björnhag and
87 Snipes, 1999; Hirakawa, 2001). However, different types of faeces were also described for
88 beavers (*Aplodontia rufa*) (Hirakawa, 2001) and nutria (*Myocastor coypus*) (Takahashi and
89 Sakaguchi, 1998), guinea pigs (Holtenius and Björnhag, 1985), capybaras (Mendes et al.,
90 2000), dassie-rats (*Pteromus typicus*) (Mess and Ade, 2005), and tuco-tucos (*Ctenomys*
91 *talarum*) (Martino et al., 2007). Nevertheless, less easily identifiable cecotrophs in rodents are
92 a reason why the CSM of lagomorphs is considered more efficient than that of rodents
93 (Björnhag and Snipes, 1999). Differences between the CSM, other than those in fluid passage
94 and visual appearance of the caecotrophs, have not been addressed so far.
95 The objective of the present study was, therefore, to compare diet selection, digesta
96 retention, digestibility and calculated gut capacity in rabbits and guinea pigs as
97 representatives for lagomorphs and rodents, respectively. Although a direct comparison of the
98 two species has been published previously (Sakaguchi et al., 1987; 1992), this was done using

99 a complete and pelleted feed. In contrast, we compared the species on a hay-only diet
100 reflecting more their natural diet.
101
102 **Materials and methods**
103 Six pygmy rabbits (body mass 1.57 ± 0.31 kg) and six guinea pigs (0.79 ± 0.07 kg) were
104 housed individually at 20 ± 2 °C on a 12 h light : 12 h dark schedule in cages (55 x 53 x 60
105 cm for guinea pigs and 97 x 60 x 55 cm for rabbits) with a carton-covered floor. Coprophagy
106 was not prevented, or accounted for, in the present study. The animals were offered grass hay
107 at *ad libitum* access. The hay contained (g/kg dry matter (DM)) organic matter, 926; crude
108 protein, 72; neutral detergent fibre (NDF), 635; and acid detergent fibre (ADF), 360 as
109 analysed in two subsamples by standard procedures (AOAC, 1997). Fresh water was
110 available at all times. After 2 weeks of adaptation, intake (food offered and leftover) was
111 registered daily, and faeces were collected completely for 7 days at regular intervals (from 4 h
112 at the beginning up to 12 h on the last day). Faeces were dried to constant weight. These
113 individual faecal samples were used for passage marker analysis (see below). From these
114 samples, a representative pool sample was prepared for the analysis of faeces for DM, total
115 ash, crude protein, NDF, ADF and gross energy (AOAC, 1997). From these data apparent
116 digestibility of nutrients and energy were calculated as

117 (Intake – excretion) / intake × 100.

118 Mean ingesta retention times (MRT) were determined by feeding a particle (chromium-
119 mordanted fibre, < 2 mm) and a fluid/solute (cobalt-EDTA) marker prepared according to
120 Udén et al. (1980). Marker analysis followed the procedure outlined by Behrend et al. (2004)
121 and Hummel et al. (2005); in doing so, wet ashing with sulphuric acid was followed by atom
122 absorption spectroscopy. The MRT in the total gastrointestinal tract was calculated according
123 to Thielemanns et al. (1978) as

$$MRT = \sum(t_i \times dt \times c_i) / \sum(dt \times c_i)$$

where t_i = time after marker application (h), dt = time interval represented by marker concentration (calculated as $(((t_{i+1} - t_i) + (t_i - t_{i-1})) / 2)$, and c_i = faecal marker concentration at time i (mg/kg DM). The marker was assumed to have been excreted completely once the faecal Co and Cr contents were the same as before marker application. The selectivity factor was calculated as $MRT_{particles}/MRT_{solutes}$. The indigestible gut content (V_N) and the total gut content (V) were calculated according to Holleman and White (1989) as

$$V_N = F * MRT$$

where F = faeces output (kg DM/h) and MRT = the average particle passage time through the entire digestive tract (h), and

$$V= (V_N - (V_N /(1 – (aD\ DM/100)))/\ln(1 – (aD\ DM/100))$$

assuming an exponential absorption of ingested food with time spent in the digestive tract. Because of the accepted linear scaling of gut fill with body mass (reviewed in Clauss et al., 2007b), gut fill was expressed as a proportion of body mass (BM).

Comparisons between rabbits and guinea pigs were performed using a t-test in PSAW 18.0 (SPSS Inc., Chicago, IL). The significance level was set to 0.05.

Results

On a metabolic body mass basis ($BM^{0.75}$), the rabbits tended ($p < 0.1$) to ingest less hay than the guinea pigs (Table 1). The rabbits apparently fed more selectively than the guinea pigs and the leftover of the hay offered was higher ($p < 0.05$) in NDF and ADF. Note that unexpectedly, crude protein levels also were higher in leftovers than in the offered hay, but there was no significant difference between the species. The rabbit faeces contained more ADF ($p < 0.05$) than guinea pig faeces, whereas their crude protein content was not significantly lower. Fibre digestibilities were lower in the rabbits than in the guinea pigs; they also tended ($p < 0.1$) to express lower DM and OM digestibility. The apparent digestibility of

protein did not differ between the species. Whereas MRT of particles did not differ between the species, rabbits had drastically longer ($p < 0.001$) MRT of solutes than guinea pigs. The passage pattern of the markers showed a parallel movement of solute and particle markers in the guinea pigs, but a distinct separation between particles and solutes in the rabbits (Fig. 1). This pattern was consistent for all individuals of each species. Consequently, the calculated selectivity factor was very low in rabbits at 0.30 (95% confidence interval: 0.28 to 0.33) (Table 1). In guinea pigs, the selectivity factor was just above 1.0 (mean: 1.18, 95% confidence interval: 1.04 to 1.30). In both species, recurrent marker peaks were consistent with an assumed re-ingestion of the markers via coprophagy. The calculated DM gut fill was lower ($p < 0.01$) in the rabbits than in the guinea pigs.

Discussion

The fundamental differences in solute and particle passage patterns between rabbits and guinea pigs described previously for animals fed on pelleted compound feeds (Sakaguchi et al., 1987; Sakaguchi et al., 1992) are obviously also present in forage-only fed animals. The passage patterns as observed in the guinea pigs of the present experiment have been found in several other rodent species with anatomical features of a 'mucous-trap' CSM (Pei et al., 2001). Recurrent marker peaks, considered typical for coprophagy (Clauss et al., 2007a), were evident in both species. The present experiment confirms previous findings on lower apparent digestibility of DM and, in particular, fibre fractions in rabbits than in guinea pigs (Slade and Hintz, 1969; Sakaguchi et al., 1987; Sakaguchi et al., 1992). In contrast, there was no higher apparent crude protein digestibility and no lower protein contents in the hard faeces of rabbits as compared to that of guinea pigs as had been reported previously for rabbits in comparison with other rodents with a mucous-trap CSM (Slade and Hintz, 1969; González-Jiménez and Escobar, 1975; Sakaguchi, 2003). Furthermore, the general assumption that lagomorphs exhibit a particularly high protein digestibility (Monk, 1989) could not be corroborated by the

176 present study, even though rabbit faeces contained numerically less crude protein than guinea
177 pig faeces.

178 The present study illustrated that rabbits feed more selectively than guinea pigs, potentially
179 due to their inherently lower capacity to digest fibre, and that rabbits have a lower DM digesta
180 load than guinea pigs per unit body mass. A similar difference results when the data from
181 Sakaguchi et al. (1987) on food intake, digestibility and particle retention of rabbits and
182 guinea pigs on a pelleted compound feed are used to calculate DM gut fill (22.6 vs. 31.5 g/kg
183 BM in rabbits vs. guinea pigs, respectively).

184 Measurements of a solute marker, such as Co-EDTA, are traditionally interpreted as 'fluid
185 retention' or 'fluid passage' (e.g. Pickard and Stevens, 1972). Thus the pattern shown in Fig.
186 1 could be paraphrased as indicating a longer 'fluid retention' in rabbits than in guinea pigs.
187 However, the interpretation that fluids are selectively retained in a 'wash-back' CSM is
188 problematic. Clauss et al. (2010b) explained that retention times measured for fluid passage
189 markers do not actually represent retention of fluid. In the passage of the digesta through the
190 gastrointestinal tract, fluid is constantly absorbed and excreted from and to the gut. The fluid
191 excreted in the faeces therefore does not quantitatively represent a fraction of the fluid
192 ingested via food or drinking water, but rather the last fraction of fluid excreted into the
193 digesta and not absorbed from the distal colon. Because a fluid passage marker is, by
194 definition, not absorbable, it is 'passed on' from one fluid fraction to the next. Excessive
195 dosages of fluid passage markers can even lead to diarrhoea because the marker binds an
196 excessive amount of water which remains in the intestinal tract (Bernard et al., 1995).
197 Because the term 'fluid retention' presumably does not describe a physiological process, we
198 advocate the use of the term 'solute retention', following Cork et al. (1999).

199 The behaviour of a solute marker, in comparison to the particle phase of digesta, represents
200 the amount of fluid washing of that particle phase. The true importance of the solute marker
201 may therefore consist in describing a type of washing which may be important to separate

202 different digesta phases (Lentle et al., 2006) in order to enhance solute uptake at the luminal-
203 intestinal border, or to separate very small particles (such as bacteria) from the total
204 gastrointestinal contents. Secretion of fluids into, and washing of, the digesta can occur in
205 both directions – aborad and orad. In many large mammalian herbivores, particularly in the
206 grazing species, the MRT of solutes is often shorter than that of particles (Steuer et al., 2010),
207 which indicates a particular washing of the particulate digesta phase with fluids in an aborad
208 direction allowing the fluid marker to be transported faster than the particle marker. For
209 ruminants, it has been suggested that this washing of the digesta with fluid in the forestomach
210 leads to a particularly efficient harvest of microbes growing in the digesta (Clauss et al.,
211 2010a). The 'wash-back' CSM of rabbits, with active fluid secretion in the proximal colon,
212 retrograde fluid transport and fluid re-absorption in the caecum (Björnhag, 1972) probably
213 has a similar effect in transferring solutes and very small particles back into the caecum (Jilge,
214 1982). In analogy to ruminants, a retrograde flushing of the digesta might therefore be very
215 useful to harvest microbes growing on soluble and insoluble cell wall constituents in the
216 colonic digesta plug.

217 Different from that fluid is constantly absorbed in the colon in guinea pigs, as is indicated
218 by a monotonous increase in digesta DM content along the whole colon (Holtenius and
219 Björnhag, 1985). Due to similar reported solute and particle retention patterns, a similar
220 situation can be assumed for other caviomorph and myomorph rodents (Pei et al., 2001). It
221 can be assumed that the 'mucus-trap' CSM is less efficient than the 'wash-back' CSM due to
222 a slower extraction of bacteria from the colonic digesta plug. This could translate into the
223 necessity of a proportionately larger colon section in herbivorous rodents compared to
224 lagomorphs to achieve a sufficient degree of bacteria extraction. This hypothesis thus
225 warrants investigation, but fits well to the comparatively lower DM gut loads calculated for
226 rabbits. The distance to the groove is a crucial factor that determines the efficiency of protein
227 extraction in the 'mucous-trap' CSM. This is obvious from findings in nutria that showed that

only the part of the colonic digesta plug that is close to the colonic groove is depleted of protein, whereas the digesta in the opposite portion of the plug retains a higher protein content (Takahashi and Sakaguchi, 2000). Still, the putative difference in efficiency between the CSM types need not necessarily – as suggested for example by Hörnicke (1981) – translate into a digestive advantage of the 'wash-back' CSM.

A slower, and potentially less complete, removal of bacteria from the digesta plug in a larger colon probably explains the higher digestibility of fibre from the same feed in guinea pigs and other herbivorous rodents as compared to rabbits, even though particle retention times are not distinctively different (Sakaguchi, 2003). The more selective feeding behaviour in rabbits, as found in this study, may be the response to counterbalance the lower capacity for fibre digestion. If the 'wash-back' CSM of the lagomorphs is really associated with comparatively lower gut loads, it might help explain a peculiarity of this order: lagomorphs can run faster than other similar-sized mammals (Garland, 1983; Lovegrove, 2004). Apart from adaptations of metabolism and limb anatomy, a limited gut load (to reduce overall body mass) will contribute to this characteristic.

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Table 1 Mean (±SD) body mass, food intake, digestibility and methane production in rabbits and guinea pigs (n=6 per species)

Species	Rabbit	Guinea pig	p-value*
Body mass (BM, kg)	1.57 ± 0.31	0.79 ± 0.07	0.001
Dry matter (DM) intake (g/kg$^{-0.75}$ BM/day	50 ± 5	59 ± 11	0.076
Composition of ingested hay (g/kg DM)			
Organic matter	932 ± 2	937 ± 10	0.339
Crude protein	69 ± 2	69 ± 3	0.936
Neutral detergent fibre	613 ± 16	634 ± 2	0.025
Acid detergent fibre	331 ± 19	351 ± 7	0.054
Composition of leftovers (g/kg DM)			
Organic matter	889± 21	856 ± 33	0.065
Crude protein	82 ± 10	87 ± 10	0.462
Neutral detergent fibre	721 ± 21	642 ± 31	<0.001
Acid detergent fibre	477 ± 38	429 ± 33	0.043
Faeces composition (g/kg DM)			
Crude protein	99 ± 23	117 ± 10	0.112
Neutral detergent fibre	760 ± 66	733 ± 15	0.347
Acid detergent fibre	489 ± 09	468 ± 16	0.020
Apparent digestibility (proportion of intake)			
Dry matter	0.55 ± 0.06	0.61 ± 0.03	0.075
Organic matter	0.56 ± 0.06	0.62 ± 0.03	0.072
Crude potein	0.37 ± 0.09	0.35 ± 0.06	0.570
Neutral detergent fibre	0.44 ± 0.10	0.55 ± 0.05	0.038
Acid detergent fibre	0.34 ± 0.10	0.48 ± 0.06	0.014
Mean retention times (h)			
Particles	15 ± 3	18 ± 6	0.286
Fluid (Solutes)	51 ± 9	16 ± 4	<0.001
Selectivity factor	0.30 ± 0.03	1.18 ± 0.17	<0.001
Gut fill (g DM/kg BM)	19.6 ± 4.7	29.7 ± 4.1	0.003

*Independent sample t-test.

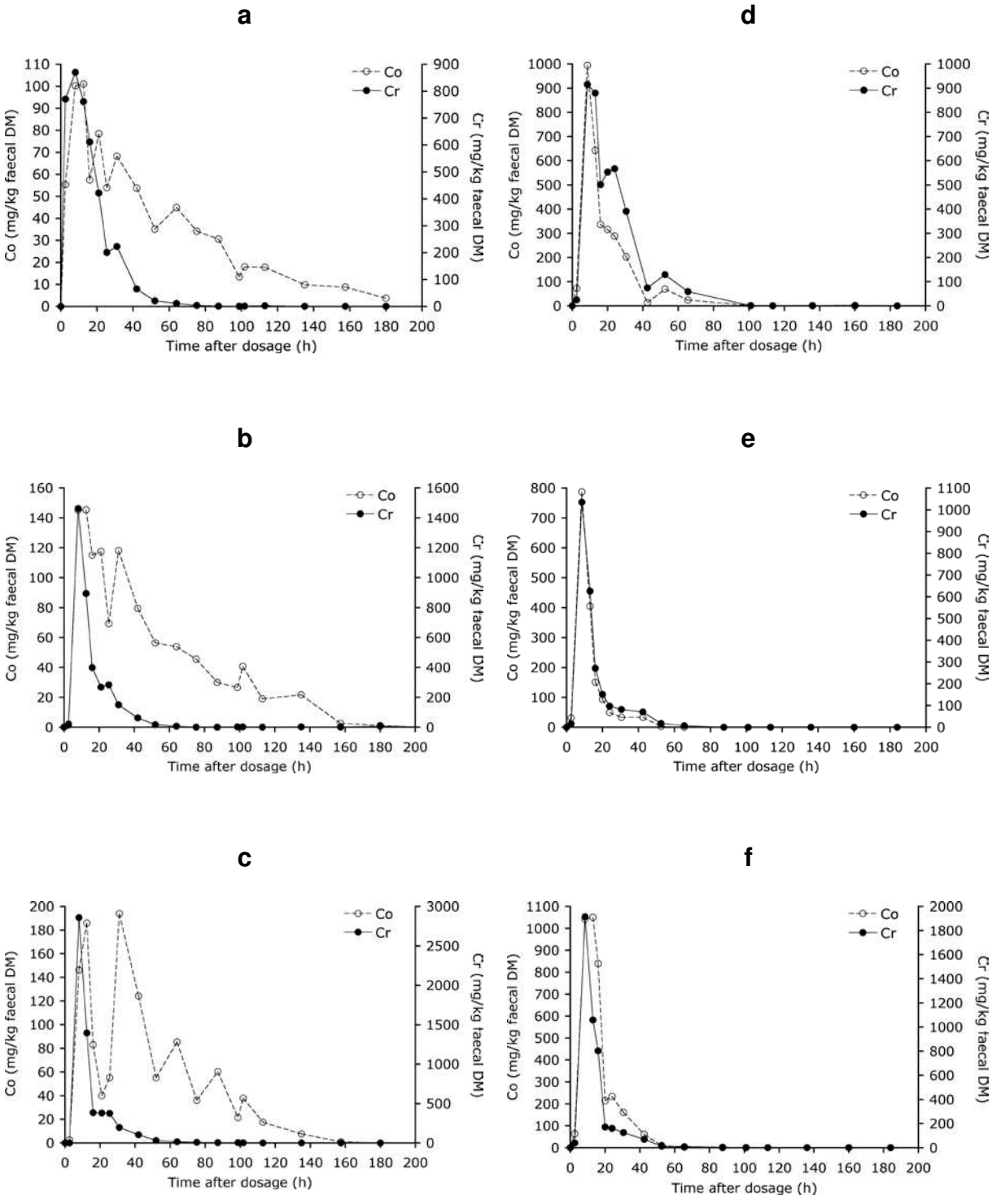

Figure 1 Faecal excretion pattern of solute (Co) and particle (Cr, < 2 mm) markers in three individual rabbits (a-c) and guinea pigs (d-f).